

mainly for the attachment of the muscles that move the thoracic appendages and the flexor muscles of the thorax and abdomen. In scorpions and *Limulus* a complete cartilaginous occipital ring is formed about the spinal cord, near its union with the brain. The plate is a continuous structure, and there is no indication whatever that it consists of two separate lateral bars, as maintained by Gaskell.

We recognize three parts to the endosternite of arachnids, namely, two lateral bars, a broad plate of cartilage on the dorsal side of the nervous system uniting the posterior ends of the bars, and a bridge of cartilage on the ventral side, which, together with the above-mentioned parts, forms a continuous ring about the anterior end of the spinal cord.

This whole structure, after the extensive reduction of the thoracic appendages and the muscles that move them, is retained, apparently, in the ancestral vertebrates, and becomes, as was first pointed out by Patten in '89, the primordial cranium. The lateral bars, the transverse plate, and the ventral arch correspond respectively to the trabeculae, the basilar plate, or parachordals, and the occipital ring. If we add the olfactory and auditory capsules and roof over the remaining dorsal surface, we obtain a complete cartilaginous cranium like that of higher forms. As we shall show elsewhere (*American Naturalist*), Gaskell's attempt to utilize the endosternite in his version of the origin of vertebrates is a complete failure, since under the conditions of his theory it must be torn apart and put together again upside down, with the old occipital ring replaced by a new one on the opposite side of the endosternite from the one on which it actually occurs. The endosternite has a true cartilaginous consistency, and is composed of a mass of interwoven fibers containing variously formed stellate lacunae, which may be very clearly seen after macerating out the cell contents. The lacunae are united by numerous anastomosing canaliculi, which in the living cartilage contain minute branching processes of the cartilage cells situated in the lacunae.

II. The six segmentally arranged *cartilages* of the *spinal cord* (Pl. VI, Fig. 1) contain the same kind of cartilage as the endosternite. They are the forerunners, we believe, of the

segmental cartilages found in corresponding regions in primitive vertebrates, and which give rise to the vertebral column. The cartilages serve evidently as points of attachment for segmentally arranged muscles that meet at those points. But we must not conclude that that is the only reason why the cartilages are there, because cartilages are not always formed at points where muscles are attached to one another. It is obviously impossible to carry the comparison with vertebrate cartilages any farther. It is enough for our purpose to show that the conditions in *Limulus* are such as to produce a series of segmentally arranged cartilages about the spinal cord, similar to those in primitive vertebrates.

III. There are seven pairs of *branchial cartilages* composed of an entirely different tissue histologically (and chemically, also, according to Gaskell) from that in the endosternite and the segmental cartilages.

The first pair arise from the inner surface of the chilaria, and are attached to the posterior margin of the endocranium so that they appear to form a part of it. The remaining six pairs arise from the base of the abdominal appendages and go to the corresponding entopophyses. They develop, as will be shown in one of the papers of this series, at a very early embryonic period as clearly defined outgrowths of the walls of the mesoblastic somites. Their union with the epidermis is secondary, and they are in no wise derived from the modification of chitinous ingrowths from the epidermis, as maintained by Gaskell.

These branchial bars of the mesothorax correspond, we believe, to the cartilaginous bars of the visceral clefts of vertebrates, as we first indicated in '89. In '93 we called attention to the surprising histological resemblance between these cartilages and those of *Petromyzon*, and still later ('96) we showed that there was a certain number of embryos in which one or more pairs of appendages were invaginated instead of evaginated. Transverse slits were thus formed along the sides of the head, resembling vertebrate gill slits and recalling to mind the lung books of scorpions and spiders. In *Limulus* the appendages most frequently invaginated, the thoracic ones, are not provided with gills. This again is suggestive since in vertebrates

the most anterior visceral arches are likewise devoid of gill lamellae. On the neural side of each thoracic appendage of *Limulus*, except the first and last, is a large group of sense organs supplied by a special ganglionated tegumentary nerve, *i.e.*, the gustatory organs of the coxal spines (Patten, '93) and the sense organs on the endopodite of the abdominal appendages. These sense organs and nerves correspond in position and in mode of development respectively to the suprabranchial sense organs and the rami dorsali of the cranial nerves of vertebrates.

IV. *The Dermal Skeleton.*—*Limulus* is the only invertebrate where the chitinous exoskeleton has begun to form a system of true dermal bones (Patten, '94). They arise as innumerable ingrowths of the ectoderm that unite to form a mass of anastomosing chitinous trabeculae. The tissue thus formed resembles coarse cancellated bone, but more especially the coarse bony networks that form the inner layers of the cephalic shields of the *Cephalaspidæ*. Within these trabeculae are numerous cavities, which, after the shell is macerated and dried, become filled with air, and then bear a strong resemblance to true bone lacunae. They are spindle-shaped lacunae, with two or more very fine canaliculi leading off from them, which appear to unite in some cases with the canaliculi of neighboring lacunae. In living tissue the lacunae are filled with a substance resembling protoplasm, and the larger ones appear to be nucleated. Thus, an entirely new dermal structure is forming here unlike that known in any other invertebrate; namely, local ingrowths of the ectoderm, forming a network of chitinous trabeculae, into which numerous cells migrate to form true bone corpuscles.

As the trabeculae cannot be shed periodically, like the rest of the exoskeleton, they are retained permanently within the body. Since, as we now know, some forms of chitin are very closely allied to chondrin, perhaps this condition may be the means of ultimately completing the chemical metamorphosis of chitin into chondrin. But there is no evidence that other chitinous ingrowths, such as the entopophyses or the apodemes of many arthropods, are invaded by cells, or that they have

made any decided approach in chemical composition towards true bony or cartilaginous structures.

We can readily understand how such a sub-dermal framework as we see in *Limulus* might lose its connection with the epidermis, and the latter form a continuous layer above it. Then the hard superficial chitinous armor would no longer be needed, either for the attachment of muscles or for protection, and might disappear altogether, thus obviating the dangers of periodically shedding the old chitinous exoskeleton.

Thus *Limulus* appears to have laid the foundation for an elaborate system of internal supports; namely, the primordial cranium, the branchial cartilages, the cartilages of the spinal cord, and the sub-ectodermal structures which resemble dermal bones. These parts have different modes of origin, and differ widely histologically from one another, yet they agree in all essential features with the corresponding parts of the vertebrate skeleton. In vertebrates we so frequently see these structures welded together into a common framework for the whole body, that we underestimate the importance of certain facts of vertebrate ontogeny, which indicate more and more clearly that the vertebrate skeleton is also composed of several parts quite different in structure and origin.

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REFERENCE LETTERS.

<i>ab. en.</i>	abdominal endochondrite.	<i>mem.</i>	membrane to which are attached the veno-pericardiac muscles.
<i>a. c.</i>	anterior cornua.	<i>m. r.</i>	marginal ridge.
<i>a. p.</i>	anterior process of abdominal endochondrite.	<i>n.</i>	neural division of anterior cornu of plastron of Apus.
<i>apo.</i>	apodeme.	<i>n. n.⁴⁻⁸</i>	neural nerves.
<i>cap. b.</i>	capsuliginous bars.	<i>n. pl.</i>	neural plates.
<i>ch.</i>	chilaria.	<i>n. pr.</i>	neural processes.
<i>ch. m.</i>	origin of chilial muscles.	<i>oc. r.</i>	occipital ring.
<i>cr. com.</i>	cross-commissures.	<i>oe. col.</i>	oesophageal collar.
<i>f.¹⁻²</i>	foramina.	<i>op. m.</i>	origin of opercular muscles.
<i>h.</i>	haemal division of anterior cornu of plastron of Apus.	<i>p. p.</i>	posterior processes of abdominal endochondrite.
<i>h. n.⁴⁻⁸</i>	haemal nerves.	<i>p. pr.</i>	posterior process.
<i>h. p.</i>	haemal processes of abdominal endochondrite.	<i>s.</i>	shoulder joining latero-posterior processes.
<i>h. pr.</i>	haemal processes of plastron.	<i>v. p. m.¹⁻²</i>	veno-pericardiac muscles.
<i>in. n.⁶⁻⁸</i>	intestinal nerves.	<i>w., x., & y.</i>	points of muscular attachment on plastron of Apus.
<i>int.</i>	integument.	<i>z.</i>	membrane attached to posterior side of plastron of Apus.
<i>l. c.</i>	lateral cornua.		
<i>l. p. pr.</i>	latero-posterior processes.		
<i>m.</i>	middle division of anterior cornu of plastron of Apus.		

EXPLANATION OF PLATE I.

FIG. 1. $\times 2$. Endosternite of *Limulus* from neural side, anterior extremity towards top of plate. Only the bases of the lateral cornua (*l. c.*) are represented. The anterior cornua (*a. c.*) are prolongations of the thickened sides of the plastron. The sides of the plastron are roughened by muscular attachment. Inside the marginal ridge (*m. r.*) the floor of the plastron anteriorly is smooth and marked only by the slight transverse furrows indicating the course of the fibers of the cartilage, for there are no muscles attached here except a few strands going to the oesophagus. Posterior to this space the irregular markings indicate an area of muscular attachment, the anterior limit of which is marked by a V-shaped outline. The marginal ridge (*m. r.*) runs along each side of the plastron, from the anterior cornua to the occipital ring (*oc. r.*). Anteriorly the ridge rises sharply above the floor of the plastron, but posteriorly it is only a low, rounded shoulder.

The occipital ring (*oc. r.*), shaded lighter than the rest of the plastron, is marked on the anterior margin by the attachments of muscle fibers going to the integument behind the mouth. On the top are two shallow pits (*ch. m.*) in which a pair of muscles going to the chilaria take their origin. From the posterior side of the ring thin strands of connective tissue go to the capsuliginous bars (*cap. b.*). The capsuliginous bars (*cap. b.*) arise from the thinner portion of the plastron, in the angle between the posterior process (*p. pr.*) and the latero-posterior processes (*l. p. pr.*). The posterior process (*p. pr.*) is unpaired and is divided into two divisions.

The first pair of foramina (*f.¹*) are represented by black dots at the bases of the latero-posterior processes in the thick portion of the cartilage; the second pair (*f.²*) by the light circles in the thin portion back of the occipital ring.

FIG. 2. $\times 2$. Endosternite of *Limulus* from haemal side. The distal ends of the lateral cornua upon the left side are disconnected from the proximal portions. These cornua are fully one-third longer than here represented. The drawing shows their mode of attachment to the haemal side of the plastron and the courses of the fibers in and about their bases. This portion of the haemal surface is free from muscles. The area of muscular attachment begins with the splintery appearance just anterior to the haemal processes (*h. pr.*). The edges of the plastron between the lateral cornua and the haemal processes are slightly elevated. The haemal processes (*h. pr.*) are stout and rise a considerable distance above the body of the plastron.

The first pair of foramina (*f.¹*) appear as dark slits a short distance behind the haemal processes.

The posterior process (*p. pr.*) begins as a low ridge in the median line opposite the haemal processes. Each division of its forked end is deeply grooved. The capsuliginous bar (*cap. b.*) on the left is shown entering the base of one of the chilaria (*ch.*), to the posterior side of which it is attached. Running along the left side of the plastron is a connective tissue membrane (*mem.*) to which the venopericardiac muscles are attached. The bases of the two anterior of these muscles (*v. p. m.¹⁻²*) are represented. Neural to the base of the second muscle (*v. p. m.²*) the membrane is attached to the integument (*int.*) by a bundle of connective tissue

fibers. Alongside the chilaria it is attached to the integument by a similar bundle of connective tissue.

FIG. 3. $\times 2\frac{1}{2}$. Posterior portion of plastron of *Limulus* and first abdominal endochondrite, with posterior half of oesophageal collar (*oe. col.*) and nerves, neural side. Four of the cross-commissures (*cr. com.*) are shown. In each neuromere are two pairs of nerves—a neural pair (*n. n.⁴⁻⁸*) and a haemal pair (*h. n.⁴⁻⁸*). Of the neural nerves, *n. n.⁴*, *n. n.⁵*, and *n. n.⁶* supply the fourth, fifth, and sixth pairs of legs respectively; *n. n.⁷*, the chilaria; and *n. n.⁸*, the operculum. All the haemal nerves supply the skin of the carapace and other organs; *h. n.⁶* and *h. n.⁷* give off small nerves (*in. n.⁶* and *in. n.⁷*) through the first and second pairs of foramina (*f.¹* and *f.²*) respectively; *h. n.⁸* also gives off a small nerve (*in. n.⁸*) just posterior to the plastron. This is seen through the semi-transparent connective tissue attached to the capsuliginous bars. These small nerves (*in. n.⁶⁻⁸*) communicate with the sympathetic system supplying the intestine and longitudinal abdominal muscles. The nerves *n. n.⁷⁻⁸*, *h. n.⁷⁻⁸*, and the ventral cord (*v. c.*) pass through the occipital ring. The ventral cord passes haemal to the abdominal endochondrites, the first of which (*ab. en.*) lies at the base of the operculum. The shallow pits (*op. m.*) on the surface of this endochondrite, similar to those on the occipital ring, represent the attachments of a pair of muscles entering the operculum. Posterior and anterior to these pits the endochondrite is in contact with the integument. In some cases the anterior and posterior processes (*a. p.* and *p. p.*) of successive endochondrites are continuous with each other as thin strands of connective tissue. The haemal processes (*h. p.*) which straddle the ventral cord give attachment to haemo-neural muscles.

FIG. 4. $\times 2$. Endosternite of *Limulus* from posterior side, showing the occipital ring (*oc. r.*) and its relation to the nerves. The portion of the plastron anterior to the occipital ring is not represented.

S. is a thickened shoulder uniting the bases of the latero-posterior processes (*l. p. pr.*). Other reference letters as in Fig. 3.



EXPLANATION OF PLATE II.

FIG. 5. $\times 45$. Endosternite of *Apus*, neural side, anterior extremity towards top of plate. The jagged ends (*m.*) furnish attachment for the muscles of the mandibles. The anterior cornua (*a. c.*) are each divided into three parts (*h.*, *m.*, and *n.*). A pair of chitinous apodemes (*apo.*) project into the endosternite on the posterior side. Muscles going to the maxillae are attached to the small processes at *x*. A few strands going to the integument are attached at *y*. The process *z* is a thin membrane attached to the integument between the longitudinal commissures of the ventral cord.

FIG. 6. $\times 45$. Endosternite of *Apus*, haemal side. Longitudinal abdominal muscles are attached to the jagged processes (*w.*) on the posterior side. Other reference letters as in Fig. 5.

FIG. 7. $\times 60$. Sagittal section of endosternite of *Apus* near median line; anterior end towards the right of figure. It shows the neighboring integument (*int.*) with the muscles going to it from *y*, the relations of the membrane *z* to the integument, and the positions of the cross-commissures (*cr. com.*¹⁻³) with reference to the endosternite.

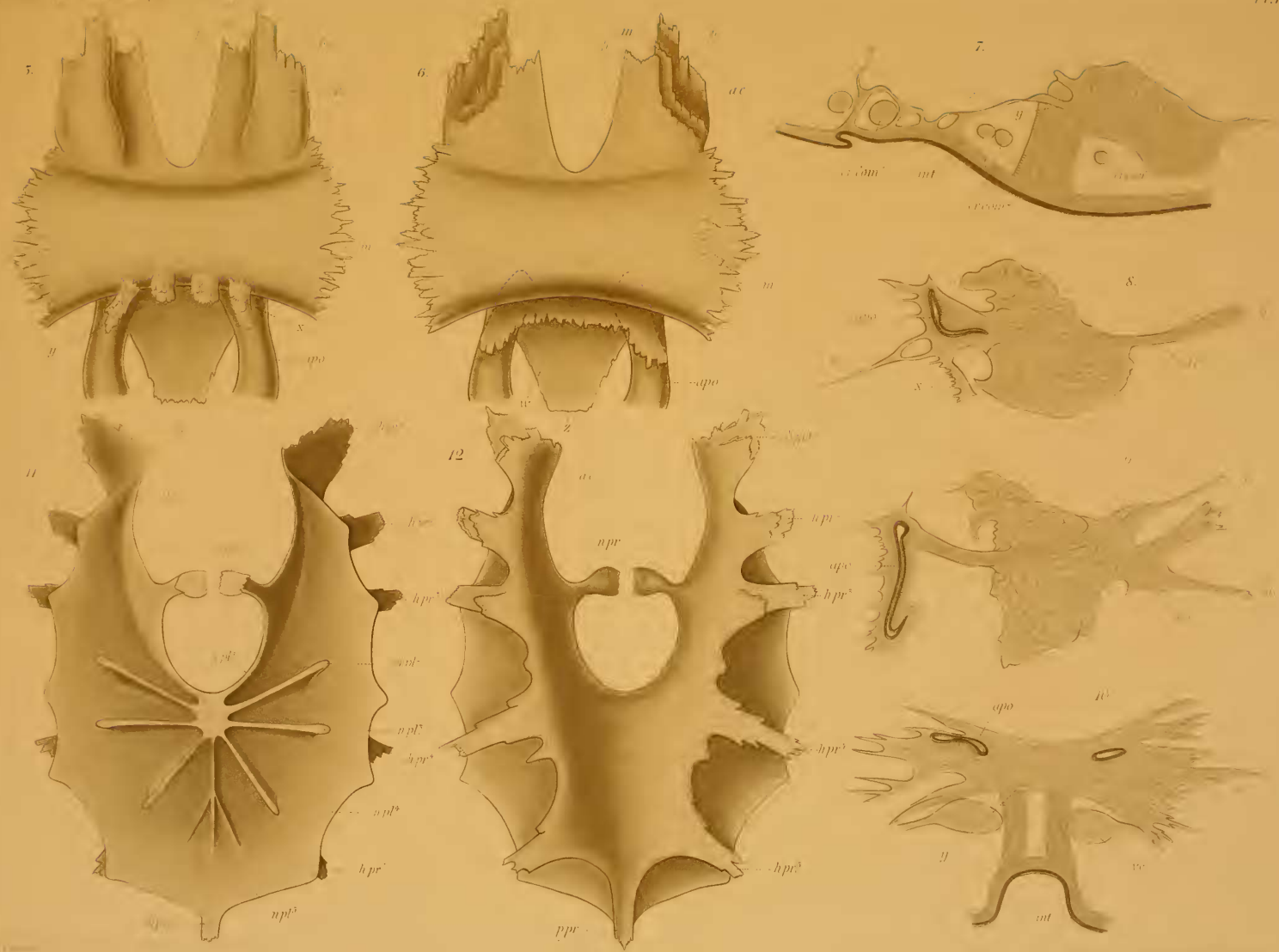
FIG. 8. $\times 60$. A section of the plastron of *Apus* a little farther from the median line than the preceding. It shows the apodeme (*apo.*) and the tendinous cord running from it, through the plastron, to the anterior cornu (*a. c.*). The process *x*, the membrane *z*, and the projections due to attachment of abdominal muscles to posterior side of apodeme are cut by this section.

FIG. 9. $\times 60$. A section of the plastron of *Apus* still farther from the median line. The apodeme (*apo.*) is approaching the exterior. All three divisions (*h.*, *m.*, and *n.*) of the anterior cornu (*a. c.*) are cut through.

FIG. 10. $\times 60$. A cross-section through posterior part of plastron of *Apus*. It cuts the inner ends of the apodemes (*apo.*), the muscles at *y*, and a pair of ganglia of the ventral cord (*v. c.*).

FIG. 11. $\times 10$. Endosternite of *Mygale*, neural side. The anterior cornua (*a. c.*) are very large. The neural processes (*n. pr.*) are in contact with the integument. The neural plates (*n. p.*¹⁻⁵) project vertically from the body of the plastron. The ends of the five haemal processes (*h. pr.*¹⁻⁵) protrude beyond the edges of the plastron. The posterior process (*p. pr.*) is not cleft, as in *Limulus*.

FIG. 12. $\times 10$. Endosternite of *Mygale*, haemal side. Five pairs of haemal processes (*h. pr.*¹⁻⁵) rise from the sides of the hollow in which the intestine lies. Reference letters as in Fig. 11.



A CONTRIBUTION ON THE MINUTE ANATOMY OF THE SYMPATHETIC GANGLIA OF THE DIF- FERENT CLASSES OF VERTEBRATES.

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INTRODUCTION.

EVEN a cursory review of our knowledge of the minute anatomy of any tissue or organ teaches us that the various steps in the perfection of our knowledge are in a large measure synchronous with advances made in microscopical technic. This is, perhaps, to no one more clearly shown than to him engaged in neurological work. The introduction of solutions of osmic acid and gold chloride, the Weigert's haematoxylin method, the methods of Golgi and Ehrlich, and the numerous other special methods, have, each in its turn, directed the attention of investigators to results hitherto unattained. This is especially true of the chrome silver and the methylene blue method; the results obtainable by these two methods, variously modified (embracing, as they do, a large portion of our more exact knowledge of the shape of neurons, and especially of their relation to each other and to the myriads of cells under their influence), have led many workers to devote much of their time to the investigation of various portions of the central and peripheral nervous system of vertebrates, and to some extent, also, of the still larger group of invertebrates. Of this number many, no doubt, encouraged by the earlier results of Kölliker and Ehrlich, have used these methods for the investigation of the sympathetic or ganglionic nervous system. And it is gratifying to reflect that the researches of Kölliker, Ehrlich, Aronson, Arnstein, Smirnow, Cajal, Van Gehuchten, V. Lenhossék, Sala, Retzius, d'Erchia, Dogiel, and others have very much broadened our knowledge concerning this system, many points having been observed so often that they are beginning to be accepted as demonstrated facts.

My reason for presenting the following research may, if such reason be required, be briefly stated as follows :

It seemed to me desirable to confirm some of the observations previously made, with what seemed to me somewhat improved histological methods, hoping at the same time to throw new light on some of the still disputed questions, and especially to broaden our knowledge of these structures by systematically investigating the sympathetic ganglia of types from the several classes of vertebrates, using in each case the same methods.

During the investigation, material was obtained from the following vertebrates :

FISHES.

Ambloplites rupestris (Raf.), rock bass.
Micropterus dolomieu (Raf.), small-mouth black bass.
Perca flavescens (Mitch.), perch.

AMPHIBIA.

Rana Catesbiana. *Rana* Hal.

REPTILIA.

Chrysemys picta. *Chelydra serpentina*.
Emys meleagris.

BIRDS.

Gallus domesticus — chicken.

MAMMALIA.

Dog, cat, rabbit, and guinea pig.

The subject-matter to be discussed in this research will be taken up as follows :

- 1) A brief discussion of the methods used.
- 2) A descriptive account of the results obtained in the preparations made from each of the above classes of vertebrates, in the order above named, with the literature bearing on the subject.
- 3) The general conclusions which may be drawn.

Method.

In the earlier portion of this work both the chrome silver and the methylene blue method were used ; the former was, however, soon discarded, owing to its greater uncertainty ;